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Mesopredator Detection and Eastern Spotted Skunk Den Site Selection in North Carolina

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MESOPREDATOR DETECTION AND EASTERN SPOTTED SKUNK DEN SITE SELECTION IN NORTH CAROLINA

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ABSTRACT

Small carnivore assemblages have been a topic of interest for many years because of their potential top-down effect on communities. However, mesopredators are a challenge to investigate because of their small sizes and elusive behavior. Advances in technology, such as non-invasive trail cameras and smaller GPS tracking devices, have increased the success in monitoring these communities, and we are learning that some of these species' populations have drastically declined, are currently declining, or the population status is unknown.

Adding an attractant to remote camera sites has become a popular method to increase detections of mesopredators. However, there is an ongoing debate about whether or not baiting remote cameras biases the behavior and detection of these species. We investigated how baiting remote cameras with canned sardines affects mesopredator detection probabilities and temporal activity in two areas in North Carolina. We used an experimental design in which we baited half our camera sites and then switched the unbaited and baited camara sites halfway through the survey season. We estimated detection probability for each species using occupancy models, and we used kernel density estimations to evaluate changes in temporal activity at baited and unbaited sites. We found that baiting remote camera stations increased the detectability for coyotes, raccoons, opossums, and eastern spotted skunks by up to 5 times but had little or no effect on bobcats and striped skunks detectability. Moreover, baiting camera sites did not alter the temporal activity of the species we most frequently detected (coyotes, raccoons, and opossums). Our results suggest that the efficacy of baiting remote cameras to increase carnivore probability of detection is species-specific, and despite increasing the total number of detections, using baits generally does not bias species temporal behavior.

Managing for eastern spotted skunks (*Spilogale putorius*) is of particular interest because of the large population declines since the 1940s. We investigated how fine-scale habitat features influenced eastern spotted skunk den site selection in two areas in North Carolina. We radio-tracked spotted skunks from January-August 2018-2020. We identified two available den sites for every used den site and assessed selection using discrete choice models. Male spotted skunk den selection was associated with a broad range of variables including low basal area, high canopy closure, closer distances to drainage channels, low forb and grass groundcover, larger den entrance sizes, and steeper slopes. Female spotted skunk den selection was associated with low basal area and rocky outcrop substrates. Our findings suggest that predation and competition could be strong drivers of spotted skunk den site selection and highlight the importance of managing forests for vegetative cover and closure to increase den site availability for eastern spotted skunks.

DEDICATION

I dedicate this thesis to my father for his fighting spirit. You have given so much support even while battling through throat cancer and have shown me true strength and courage. I will always be by your side as we fight this together no matter how far away I may be.

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CHAPTER 1

EFFECTS OF BAITING REMOTE CAMERA SITES ON MESOPREDATOR DETECTION AND ACTIVITY IN NORTH CAROLINA

INTRODUCTION

Carnivores tend to move across large areas and frequently interact with each other and other species, so large-scale studies are often necessary to understand carnivore assemblages. However, these large-scale studies are difficult to execute because of low detection probability associated with cryptic or low-density species occupying large areas. Remote camera studies are a noninvasive method that can be used to monitor and investigate carnivores (Gompper et al. 2006, Robinson et al. 2017), are relatively easy to deploy, and tend to require less labor and time in the field than traditional invasive techniques such as live capture (Kays and Slauson 2008). Managers and researchers can use data from remote cameras to examine occupancy, behavior, and population density of various species (Thorn et al. 2009, Lazenby et al. 2015, Zapata-Rios and Branch 2015, Braczkowski et al. 2016). Although, some species such as *Mustela spp.* remain difficult to detect (Reed 2011, Mos and Hofmeester 2020).

Using attractants such as bait or scent lures can increase the detection rates of elusive carnivores (Hackett et al. 2007, Webster and Beasley 2019), but there is concern that using attractants might bias species activity, resource use, and movement. Holinda et al. (2020) suggests that sites with attractants might increase detections because the attractant influences the predators' behaviors and changes their movement patterns to search for the attractant. This behavioral change might result in finding species in locations they usually do not occupy. However, Stewart et al. (2019) suggests that baiting cameras has a weak effect on fisher (*Pekania pennanti*) movement and that landscape features may be more important for movement. Using an attractant at a remote camera station likely has species-specific effects, including having no influence or reducing detections (Mills et al. 2019, Holinda et al. 2020). Species interactions and the type of attractant used might explain decreases in detections for certain target or non-target species (Lesmeister et al. 2015, Webster and Beasley 2019, Fidino et al. 2020). Furthermore, these interactions may explain how baiting a camera station could alter the temporal activity of a species (Bischof et al. 2014, Lazenby et al. 2015, Zapata-Rios and Branch 2015) because some species may want to avoid interacting with one another. Understanding how using attractants influences species behavior is important because it could alter spatial and temporal patterns which would affect inferences of species distributions, resource utilization, abundance, density, and temporal activity.

The southeast region of the US contains a wide diversity of small carnivores (hereafter mesopredators) and researchers in this region have been using large-scale remote camera studies to monitor mesopredators, particularly eastern spotted skunks (*Spilogale putorius*). Spotted skunk baited camera array studies are widespread occurring in SC (Wilson et al. 2016, Eng and Jachowski 2019b), MO and AR (Hackett et al. 2007, Higdon and Gompper 2020), VA (Thorne et al. 2017), AL (Sprayberry and Edelman 2018), and TX (Avrin et al. In press), and these studies often use canned sardines as bait. In addition, for the past four years the North Carolina Wildlife Resources Commission (NCWRC) has deployed remote cameras to monitor mesopredators and baiting the cameras with canned sardines. The NCWRC study represents one of the largest-scale and longest-running camera-based survey efforts to date for spotted skunks and other carnivores in the Southeast. However, the effect of bait has not been investigated on the detection of mesopredators in North Carolina. As noted above, using attractants may lower detection probability (Lesmeister et al. 2015, Zapata-Rios and Branch 2015), increase the detection probability, or have no effect depending on the dynamics of the carnivore community (Webster and Beasley 2019, Fidino et al. 2020, Holinda et al. 2020). Thus, evaluating the influence of attractants is important because of the different effects it may have on inferences about the NC mesopredator community including potential biases of resource use and activity patterns.

In this study our goal was to investigate the influence of baiting remote camera locations with canned sardines on mesopredator detection and temporal activity during winter and spring in western North Carolina. Using remote cameras in the southern Appalachian region in North Carolina, our objectives were:

1. Assess how bait and other fine-scale factors might influence detection of mesopredators (skunks, coyotes, weasels, foxes, bobcats, opossums, and racoons) from mid-January through April 2020.
2. Evaluate the effects of bait on the temporal activity behavior of each species.

We hypothesized that using bait at camera sites (Schlexer 2008, Eng and Jachowski 2019a), camera station setup (Mills et al. 2019), seasonality (Hackett et al. 2007, Webster and Beasley 2019), and vegetation (Thorn et al. 2009, Eng and Jachowski 2019a) would strongly affect detection probabilities for each species (Table 1). Our study will inform the extent to which NCWRC can use baited cameras to gain inference on mesopredator detection and behavior in the long-term monitoring camera study and may be a guide for other remote camera studies considering the use of bait.

METHODS

Study Area

From mid-January to the end of April 2020, we set up a camera array in two areas of North Carolina (DuPont State Recreational Forest and South Mountains State Park) known to contain a diverse assemblage of mesopredators, including two of the less frequently detected species: long-tailed weasel (*Mustela frenata*) and eastern spotted skunk (*Spilogale putorius*; Detweiler et al. In press). DuPont State Recreational Forest (hereafter DuPont) and South

Mountains State Park with the surrounding Foothills Conservancy lands (hereafter collectively termed South Mountains) are located in the Blue Ridge region of the Appalachian Mountain Range (Figure 1). DuPont ranges from about 701 to 1097 m (2300-3600 ft) in elevation and South Mountains ranges up to 914 m (3000 ft). Both areas primarily consist of mixed deciduous forests with some evergreen species including Mountain Laurel (*Kalmia latifolia*) and Rhododendron (*Rhododendron spp.*). During the field season (January – April 2020), DuPont had a monthly average temperature range from 5.3°C to 15.2°C, and South Mountains monthly average temperature ranged from 6.2°C to 16.3°C in 2020 (National Centers for Environmental Information, https://www.ncdc.noaa.gov/). The monthly total precipitation for the DuPont area ranged from 10 cm to more than 25 cm, and the South Mountains area ranged from 5 cm to 20 cm in 2020 (National Centers for Environmental Information, https://www.ncdc.noaa.gov/).

Experimental Design

We created a grid with 2.25 km^2 (1.5 km x 1.5 km) cells across both study areas. This spacing is used by the NCWRC's long-term remote camera study and was used for other mesopredator studies (Bischof et al. 2014, Lazenby et al. 2015, Eng and Jachowski 2019a) to limit detections occurring from the same individual of each carnivore (particularly spotted skunks) at multiple remote camera sites. We set out cameras in the center of each grid cell, so that each camera was about 1.5 km apart. When the location at the center of a cell was not accessible (e.g. private property), we placed cameras up to 250 m away from the center point. There were 20 cells (20 camera locations) covering Dupont and 30 cells (30 camera locations) covering South Mountains. In each study area, we randomly assigned half of the grid cells (10 cells in DuPont and 15 cells in South Mountains) to be baited (treatment) and the other half to be unbaited (control) for the first six weeks of the full 12-week study period (Figures 2 and 3). For the last six weeks, we switched the unbaited and baited camera sites. For camera sites starting as baited during first deployment (Week 1), we nailed canned sardines in oil to a tree and left the camera deployed for the first six weeks of this deployment. Then, starting at week seven, we moved cameras with the initial bait treatment about 10-20 m away from the previous locations to avoid bias from potential remaining scents at the original location. After moving the cameras, we did not bait those new sites, thus during weeks 7-12, the now unbaited sites surveyed a similar area and were less likely impacted by any residual effect of the bait at the nearby formerly baited site. Starting at week seven, we baited the camera sites that were initially not baited during the first six weeks. We did not move the location of these unbaited to baited sites because there was no previous bait scent unlike the baited to unbaited sites.

We surveyed each site with one Bushnell Trophy Cam HD trail camera (models 119776, 119836, 119874, 119876, and 11987, Bushnell, Overland Park, KS, USA). We checked the cameras every two weeks to replenish with a new perforated can of sardines (if applicable), checked the battery life, changed out SD cards to ensure enough memory for photos, and made sure the camera functioned properly (Rocha et al. 2016, Eng and Jachowski 2019a). We used a can of sardines as bait because that matched the NCWRC study and sardines tend to be the most commonly used bait for eastern spotted skunk studies (Avrin et al. In press). We did not place the cameras on hiking trails or forest roads because of possible theft and human interference. We secured all cameras with lockboxes and cable locks. At each camera location, we recorded vegetation data within a 10 m radius within the first two weeks (i.e. before the first camera check) of each 6-week period (Table 2). We faced the camera towards a tree about 2.25-7.4 m away and positioned 40-93 cm off the ground with the exception of one camera that was 148cm off the ground because it faced down into a valley. We set all cameras to the same settings: active 24 hours a day, using an image size of 8 MP, and taking one photo per trigger with three-second intervals between triggers. At baited sites, we placed the bait 35-105 cm from the ground on a tree at least 15 cm in diameter at breast height (DBH) while facing the camera (Eng and Jachowski 2019a, Webster and Beasley 2019). We ensured that the bait tree was in the center of the photo frame. At the end of the first 6-week survey period, we switched the baited and unbaited sites and again recorded all vegetation data at the site.

Analysis

We developed 12 *a priori* hypotheses—including the global and null hypotheses—investigating effects of bait, setup conditions, and time of year on detection probability (Table 1). We predicted that treated (baited) sites and sites that were baited first would have higher detection probabilities for all species than the control (unbaited) sites (Holinda et al. 2020). We predicted that the higher the camera height, the less likely we will detect each species (Eng and Jachowski 2019a, Mills et al. 2019). We explored the influence of vegetative cover on detection probability for each species by using measurements of canopy cover and coarse woody debris (CWD). Vegetative cover is important for small carnivore predator avoidance, so we predicted higher detection probabilities in areas with higher canopy cover, and higher CWD for our smaller mesopredators (e.g. skunks, opossums, foxes; Farias et al. 2005, Lesmeister et al. 2010). However, for coyotes (*Canis latrans*) and bobcats (*Lynx rufus*) we predicted lower detection probabilities in areas with higher vegetative cover because those species are less concerned with avian predators and would likely use more open areas to travel or search for prey (Randa and Yunger 2004, Clare et al. 2015). We predicted that as the ordinal date increased (i.e. entering spring and summer seasons) we would be less likely to detect a mesopredator species because of change in movement patterns likely related to the end of the breeding season (Hackett et al. 2007, Robinson et al. 2017).

We used an information theoretic approach, Akaike Information Criterion adjusted for small sample sizes (AICc), to evaluate support for our hypotheses about mesopredator detection probability (Mills et al. 2019, Holinda et al. 2020). If the same camera captured the same species with a gap ≥ 30 minutes, we defined those events as unique detections (Bischof et al. 2014, O'Connor et al. 2017); if the interval was < 30 minutes those events were considered as one visit. Because of the very low number of detections for red foxes (*Vulpes vulpes*, n = 4) and not detecting gray foxes (*Urocyon cinereoargenteus*) or weasels (*Mustela spp*.), we excluded foxes and weasels from our analysis. For this analysis we included the coyote as a mesopredator and excluded the black bear (*Ursus americanus*) because we set out the cameras during a time of lower black bear activity to avoid damage to our baited camera sites (Eng and Jachowski 2019a). In program R (version 4.0.3; R Core Team 2020, Vienna, Austria), we used package "camtrapR" version 2.0.3 (Niedballa et al. 2020) to calculate detection histories from 12 sampling occasions (each sampling occasion was one week) for each species. We scaled and centered our quantitative covariates with a mean of zero and standard deviation of 1. To examine the effects on detection probabilities, we used package "unmarked" version 1.0.1 (Chandler 2020) to create a set of occupancy models for each species detected, and in these models, occupancy was held constant (MacKenzie et al. 2018, Mills et al. 2019). For these occupancy models (Table 2), we used the "model.select" function in the "MuMIn" package version 1.43.17 (Barton 2020) to calculate the AICc values for each model and determined our top detection models for each species based on delta AICc values and AICc weights. We identified the top model set for each species based on the 90% confidence set (Burnham and Anderson 2002, Symonds and Moussalli 2011), and selected models were above the null. We model averaged the top model sets for each species when there was evidence for model selection uncertainty. We used 95% confidence intervals to evaluate if there was an effect and the strength of the effect of the covariate on detection probability.

In addition to exploring detection probabilities of mesopredators, we investigated how baiting remote cameras influenced temporal activity for each species using non-parametric kernel density estimation (Ridout and Linkie 2009, Linkie and Ridout 2011, Wang et al. 2015). Because we rarely detected foxes, bobcats, eastern spotted skunks, and striped skunks at unbaited sites (detections < 10) we excluded these species for our temporal analysis. We used the R package "overlap" version 0.3.4 (Meredith and Ridout 2021) to estimate temporal activity as a probability density distribution using kernel density estimation for each species at baited sites and unbaited sites. From here we calculated the overlap coefficient ($\widehat{\Delta}$, area under the curve) in which a value of zero indicates no overlap – suggesting a change in temporal activity between baited and unbaited sites – and a value of one indicates complete overlap – suggesting no temporal activity alteration between baited and unbaited sites. Finally, we used Watson's two-sample test for homogeneity (Chitwood et al. 2020) in package "circular" version 0.4-93 (Lund et al. 2017) to test for significant differences in species activity at baited and unbaited sites.

RESULTS

The average number of nights surveyed was 81.84 ± 1.19 (mean ± SE, range = 43-84). Two cameras in the South Mountains area (SM11 and SM13) were active only for one day during their unbaited period, so these cameras recorded 43 active nights. Three other cameras (SM02, SM18, and SM28) in the South Mountains area had problems and only recorded 76, 82, and 68 active nights respectively. In both study areas combined, our cameras captured a total of 183 detections of raccoons (*Procyon lotor*) at 33 sites, 156 detections of opossums (*Didelphis virginiana*) at 21 sites, 107 detections of coyotes at 37 sites, 23 detections of bobcats at 15 sites, 54 detections of eastern spotted skunks at 13 sites, and 18 detections of striped skunks (*Mephitis mephitis*) at 6 sites (Tables 3a and 3b). The average latency to first detection between baited and unbaited sites were similar for all species except opossums (Table 4).

Raccoon

For our detection probability analysis, five models collectively containing all covariates made up the 90% confidence set for racoons (Table 5a). After model averaging, only the treatment covariate had a 95% confidence interval that did not overlap zero (Table 6). Using bait at our remote camera sites increased the detection probability of raccoons by about four times as much as sites without bait (from 9% to 34%; Figure 4).

For our temporal activity analysis, raccoons had a moderately high overlap (($\hat{\Delta}$ = 0.73) of activity at baited and unbaited sites. Despite this overlap, the activity periods were significantly different (W = 0.199, p-value <0.05) in which raccoon activity extended later into the morning at baited sites than at unbaited sites (Figure 5a).

Opossum

For our detection probability analysis, five models containing all of our covariates made up the 90% confidence set for opossums (Table 5b). After model averaging, only the treatment covariate had a 95% confidence interval that did not overlap zero (Table 6). Using bait at our remote camera sites increased opossum detection probability by four times as much as sites without bait (from 6% to 24%; Figure 4).

For our temporal activity analysis, opossum had moderately high overlap of activity at baited and unbaited sites ($\hat{\Delta}$ = 0.71), and the activity periods were not significantly different (W = 0.101, p-value >0.10; Figure 5b).

Coyote

In our detection probability analysis, four models containing treatment, bait order, ordinal date, and camera height made up the 90% confidence set for coyote; the null model for coyote was excluded from analysis because it did not converge (Table 5c). Treatment was the only covariate with a 95% confidence interval that did not cross zero (Table 6). Using bait at our remote camera sites more than doubled the detection probability of coyotes from 8.0% to 18.0% (Figure 4).

In our temporal activity analysis, coyote had high overlap ($\widehat{\Delta} = 0.79$) of activity between baited and unbaited sites, and the activity periods were not significantly different ($W = 0.053$, p-value >0.10; Figure 5c).

Bobcat

In our detection probability analysis, only two models containing treatment and bait order ranked above the null model and made up the 90% confidence set for bobcat (Table 5d). After model averaging, both covariates had 95% confidence intervals overlapping zero (Table 6).

Eastern Spotted Skunk

For our detection probability analysis, four models containing all of our covariates made up the 90% confidence set for the eastern spotted skunk (ESSK; Table 5e). After model averaging, only treatment had a 95% confidence interval that did not overlap zero (Table 6). On average, using bait at our remote camera sites increased eastern spotted skunk detection probability by five times as much as sites without bait (from 4% to 21%; Figure 4). Ordinal date might have had a slight positive effect on detection probability because the 95% confidence interval only very slightly surpassed zero (-0.04 to 1.39).

Striped Skunk

In our detection probability analysis, only three models containing treatment, bait order, ordinal date, and camera height ranked above the null model to make up the 90% confidence set for striped skunks (Table 5f). After model averaging, none of the covariates appeared to have noticeable effects because the 95% confidence intervals overlapped zero (Table 6).

DISCUSSION

Results from our study provide evidence that using sardines as bait at remote camera sites greatly increases the probability of detecting most mesopredator species in our system without altering their temporal activity. The detection probability of raccoons and opossums increased by about four times at baited sites compared to unbaited sites, increased by about two times as much for coyotes, and increased about five times as much for eastern spotted skunks. Bobcat and striped skunk probability of detection were minimally affected, if at all, by bait presence. When sardine bait was present, the temporal activity for raccoons subtly changed, but the other two species maintained similar temporal activity patterns. These findings support similar patterns in detection probability found by Mills et al. 2019 and Randler et al. 2020, and they support similar patterns for temporal activity found by Gerber et al. 2012 and Braczkowski et al. 2016.

The presence of sardine bait influencing all species except bobcats and striped skunks, supports species-specific responses to bait presence and bait type (Mills et al. 2019, Holinda et al. 2020). Canned sardines may not be an attractive bait for the latter two species (Iannarilli et al. 2021) resulting in less detections. Felids tend to be visual hunters and may be more attracted to visual stimuli (Cove et al. 2014). Alternatively, detectability may be considered as a function of abundance (McCarthy et al. 2013), thus fewer detections of bobcats and striped skunks may reflect relatively low densities of these species in our study areas. Therefore, we would be less likely to detect these species regardless of bait presence.

Because bait had a very strong influence on detectability for most of our species, it likely masked potential effects from other covariates in explaining the variation in our data. Previous studies evaluating detectability at baited locations or unbaited locations, found that factors such as season, weather, and vegetation may demonstrate a strong influence on detection probability. For example, O'Connor et al. (2017) found that length of season and the number of cameras in a multi-array camera study greatly increased the detection for bobcats, opossums, and raccoons without the need for bait. Even with a lure, Madsen et al. (2020) found that coyote detection was affected by weather in which detection was negatively associated with air temperature, wind speed, and precipitation and positively associated with barometric pressure. Lastly, using a bait and scent lure at camera traps, O'Connell Jr. et al. (2010) found that red fox and striped skunk detection probability was related to specific vegetation types. Thus, these factors are still important to consider in analyzing data resulting from either baited or unbaited camera sites.

Despite finding a strong effect of bait on detection probability, we found no improvement in latency to first detection for nearly all species. This suggests that canned sardines are not drawing in carnivores to camera sites more quickly or drawing in species from great distances. Rather, the higher frequency of detections and greater number of cameras (locations) that detected a species when a site was baited, suggest that once an individual found the bait, it was more likely to come back to the site. Collectively, these data suggest that use of sardines as bait is not drawing mesopredators to camera sites outside their typical home range but may support Holinda et al.'s (2020) concern of attractants changing an individual's search behavior (and resulting use of resources) within its home range. Moreover, spending more time at a bait site or in a different location when it is dangerous could be risky behavior, possibly increasing negative interactions among species (Prugh and Sivy 2020) or disease transmission (Sorensen et al. 2014). Therefore, a next step would be to investigate how baiting remote camera sites influences resource use by the mesopredator community.

Our temporal analysis suggests that using sardines as bait did not influence or only subtly influenced the temporal behavior of the most commonly encountered species (raccoon, opossum, and coyote) in our study system. Therefore, sardine-baited remote camera sites increase the frequency of detection but do not alter the time budget of when carnivores visit camera sites demonstrating that sardine-baited cameras are useful for investigating temporal interactions among these common mesopredators. The slight shift in raccoon activity to later in the morning appeared to overlap with peak coyote activity. This suggests that despite coyotes being the largest and dominant carnivore in our system (during the time period of our study), racoons did not fear coyotes enough to change their daily temporal activity (Chitwood et al. 2020). A lack of alteration in temporal activity for most species in our study could be due to our use of canned sardines as bait, which was a relatively small and difficult to consume bait compared to other studies which use a whole or partial carcass (Robinson et al. 2017, Thorne et al. 2017, Avrin et al. In press). A carcass bait is a larger and likely longer-lasting food subsidy potentially promoting more aggressive interactions among mesopredators (Allen et al. 2016), potentially leading to different temporal activity results relative to our study. We recommend site- or region-specific investigations into different types of bait and how that impacts temporal behavior because regions likely differ in seasonal food availability and carnivore community dynamics.

Collectively, our study highlights how baited camera survey efforts can benefit from dedicated investigations into the influence of bait on detection probability. Our study suggests that the detection of some species was more likely to be influenced by the use of sardines as bait than other species. This has important implications for monitoring species of conservation concern. In particular, for certain small and elusive species, like the eastern spotted skunk, detection probability and the total number of detections improved by the use of sardines as bait. In addition our findings suggest that NCWRC and other agencies planning to implement large-scale studies using this type of camera array deployment and attractant technique can be confident in using resulting data without biasing inference into temporal behavior of mesopredator communities. There are multiple ways to increase the detectability of species: using camera traps that involve bait (e.g., using whole animal carcasses as a food subsidy, Robinson et al. 2017, Thorne et al. 2017) or not using bait but placing cameras strategically in clusters (O'Connor et al.

2017) or along roads and trails (Schlexer 2008). Regardless of the methodology used, we encourage similar comparative investigations into the influence of camera setup or baiting when attempting to gain insight into the dynamics of carnivore communities. Choosing a method needs careful consideration and will largely depend on the efficacy and the resources necessary to accomplish research goals.

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TABLES

Table 1. Hypotheses and candidate models for detection probability for each mesopredator species (see footnotes for more species-specific predictions). In the predictions column, the "+" and "-" indicate the relationship between the covariate and the response variable (e.g. for "CWD", "+" denotes as CWD increases detection probability increases). If the covariate is binary (0,1) the "+" refers to higher detection probability when present or 1 while "-" refers to lower detection probability when present.

Hypotheses	Predictions	Literature
1. Treatment only	Treatment: +	Thorn et al. 2009, Eng and Jachowski 2019a
2. Treatment	Treatment: + Bait order: First:+, second: -	Thorn et al. 2009, Eng and Jachowski 2019a
3. Vegetation only	[a]Canopy cover: + [a]CWD: +	Stewart et al. 2019
4. Season	Ordinal date: -	Hackett et al. 2007, O'Connor et al. 2017, Webster and Beasley 2019
5. Camera setup and treatment	Treatment: + Bait order: First:+, second: - Cam height: -	Eng and Jachowski 2019a, Mills et al. 2019, Holinda et al. 2020
6. Season and treatment	Treatment: + Bait order: First:+, second: - Ordinal date: -	Hackett et al. 2007, Bischof et al. 2014, Webster and Beasley 2019
7. Vegetation, season, treatment	[a]Canopy cover: + [a]CWD: + Ordinal date: - Treatment: + Bait order: First:+, second: -	
8. Vegetation and season	[a]Canopy cover: + [a]CWD: + Ordinal date: -	O'Connor et al. 2017, Stewart et al. 2019
9. Vegetation, camera setup, treatment	[a]Canopy cover: + [a]CWD: + Treatment: + Bait order: First:+, second: - Cam height: -	

10. Season, camera setup, treatment	Ordinal date: - Cam height: - Treatment: + Bait order: First:+, second: -
11. Global	Treatment: + Bait order: First:+, second: - Cam height: - [a]Canopy cover: + [a]CWD: + Ordinal date: -
12. Null (intercept model)	No effect

[a]We predict that these covariates will have a negative effect on the detection probabilities for coyotes and bobcats

Table 2. Description of covariates measured to estimate mesopredator detection probability and temporal activity.

Covariate	Description
Treatment	Whether or not the camera was baited; used canned sardines in oil
Baited order	Whether the camera site was baited for first 6-week period or second 6-week period.
Camera height	Distance from ground directly below camera to the middle of the camera (cm)
Ordinal date	Ordinal date (1-366) of each sampling occasion to represent season
Canopy Cover	Averaged percent canopy coverage using a densiometer five meters out from camera tree in all cardinal directions
Coarse woody debris	Average of the counted number of downed stems >10 DBH on a 10 m by 2 m transect in all cardinal directions

Table 3. Number of detections for each species and the number of camera sites that detected each species during baited and unbaited periods in the DuPont area (a) and in the South Mountains area (b).

(a)

	Baited		Not Baited		Total	
Species	Detections	Cameras	Detections	Cameras	Detections	Cameras
Bobcat	3	1	3	3	6	3
Coyote	35	14	4	3	39	15
Opossum	111	11	10	4	121	11
Raccoon	81	10	3	2	84	10
Red Fox	4	3	0	0	4	3
Spotted Skunk	5	3	0	0	5	3
Striped Skunk	10	2	4	2	14	3

(b)

	Baited		Not Baited		Total	
Species	Detections	Cameras	Detections	Cameras	Detections	Cameras
Bobcat	14	9	3	3	17	12
Coyote	42	19	26	9	68	22
Opossum	31	8	4	4	35	10
Raccoon	82	20	17	9	99	23
Red Fox	0	0	0	0	0	0
Spotted Skunk	43	7	6	4	49	10
Striped Skunk	3	2	1	1	4	3

Table 4. Average latency to first detection for each species comparing when sites were baited and not baited (average nights ± SE).

Species	Bait	No Bait
Bobcat	18.90 ± 4.54	20.67 ± 5.04
Coyote	20.76 ± 1.92	19.58 ± 3.69
Opossum	23.42 ± 2.77	9.13 ± 1.12
Raccoon	18.63 ± 2.34	17.09 ± 3.66
Spotted Skunk	17.90 ± 4.41	21.75 ± 7.66
Striped Skunk	14.75 ± 6.65	15.67 ± 10.65

Table 5. Confidence set of models for raccoon (a), opossum (b), coyote (c), bobcat (d), eastern spotted skunk (e), and striped skunk (f). For bobcat the null model was part of the 90% confidence set and two models (M5 and M6) after the null. For striped skunk the null model was part of the confidence set and four models (M3, M5, M9, and M7) after the null. Those were taken out for model averaging. Thus bobcat and striped skunk model weights do not add up to 0.90.

(a)

Hypotheses	K	Log-Likelihood	AICc	Δ AICc	weight
Treatment only	3	-219.12	444.76	0.00	0.49
Treatment with order	4	-219.10	447.09	2.34	0.15
[a]SubGlobal 9	7	-215.71	448.09	3.33	0.09
Global	8	-214.44	448.40	3.64	0.08
Treatment and season	5	-218.69	448.74	3.98	0.07

[a]These model numbers correspond to the numbers in Table 1

(b)

Hypotheses	K	Log-Likelihood	AICc	Δ AICc	weight
Treatment and season	5	-142.13	295.62	0.00	0.31
[a]SubGlobal 7	7	-139.70	296.07	0.44	0.25
Treatment only	3	-145.36	297.24	1.62	0.14
Global	8	-139.20	297.91	2.29	0.10
[a]SubGlobal 10	6	-142.04	298.03	2.41	0.09

[a]These model numbers correspond to the numbers in Table 1

(c)

Hypotheses	K	Log-Likelihood	AICc	Δ AICc	weight
Treatment only	3	-217.15	440.83	0.00	0.34
Treatment with order	4	-216.20	441.29	0.46	0.27
Treatment and camera setup	5	-215.78	442.92	2.09	0.12
Treatment and season	5	-215.80	442.97	2.14	0.12

(d)

Hypotheses	K	Log-Likelihood	AICc	Δ AICc	weight
Treatment only	3	-84.86	176.25	0.00	0.27
Treatment with order	4	-83.73	176.36	0.11	0.26

(e)

Hypotheses	K	Log-Likelihood	AICc	Δ AICc	weight
Treatment and season	5	-82.58	176.53	0.00	0.40
[a]SubGlobal 10	6	-81.75	177.46	0.93	0.25
[a]SubGlobal 7	7	-81.02	178.71	2.18	0.13
Treatment only	3	-86.58	179.69	3.16	0.08

[a]These model numbers correspond to the numbers in Table 1

(f)

Hypotheses	K	Log-Likelihood	AICc	Δ AICc	weight
Treatment and season	5	-44.50	100.36	0.00	0.24
Treatment with order	4	-46.06	101.00	0.64	0.17
[a]SubGlobal 10	6	-43.75	101.46	1.10	0.14

[a]These model numbers correspond to the numbers in Table 1

Table 6. Coefficients after model averaging the confidence set for each species. The "x" indicates that the covariate was not in any of the confidence set models. Bolded values indicate covariates with 95% confidence intervals that do not overlap zero. Coefficients with "*" indicate that the 90% confidence interval does not overlap zero. Eastern spotted skunk is abbreviated as "ESSK" in the column heading.

Covariates	Raccoon		Opossum		Coyote		Bobcat		ESSK		Striped Skunk	
	Coef	SE	Coef	SE	Coef	SE	Coef	SE	Coef	SE	Coef	SE
Bait order (2nd)	0.03	0.20	-0.22	0.41	-0.24	0.29	-0.39	0.55	0.92	0.71	*-3.62	1.97
Camera height	0.07	0.15	-0.03	0.12	-0.02	0.07	x	x	0.11	0.22	-0.21	0.53
Canopy cover	0.08	0.19	0.07	0.20	x	x	x	x	0.03	0.15	x	x
CWD	-0.01	0.07	0.17	0.25	x	x	x	x	0.15	0.40	x	x
Ordinal date	-0.03	0.10	-0.38	0.24	0.02	0.07	x	x	*0.68	0.37	0.88	0.85
Treatment	**1.68**	0.29	**1.68**	0.39	**0.93**	0.27	*0.86	0.50	**1.90**	0.59	0.42	0.72

FIGURES

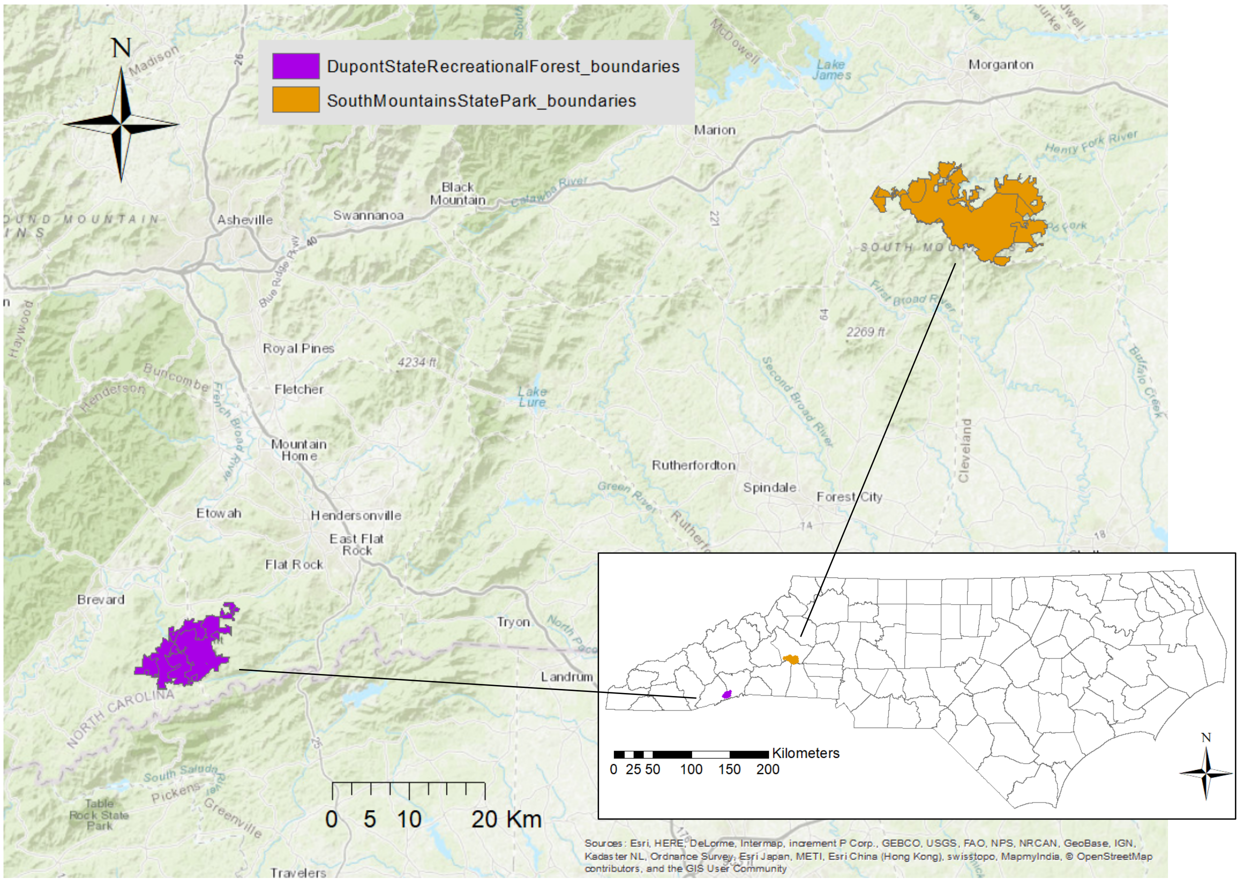

Fig. 1. Study areas in North Carolina where the smaller frame shows that our study occurred in the western region of North Carolina. The area in purple (bottom left) is DuPont State Recreational Forest and the area in orange (top right) is South Mountains State Park and Foothills Conservancy.

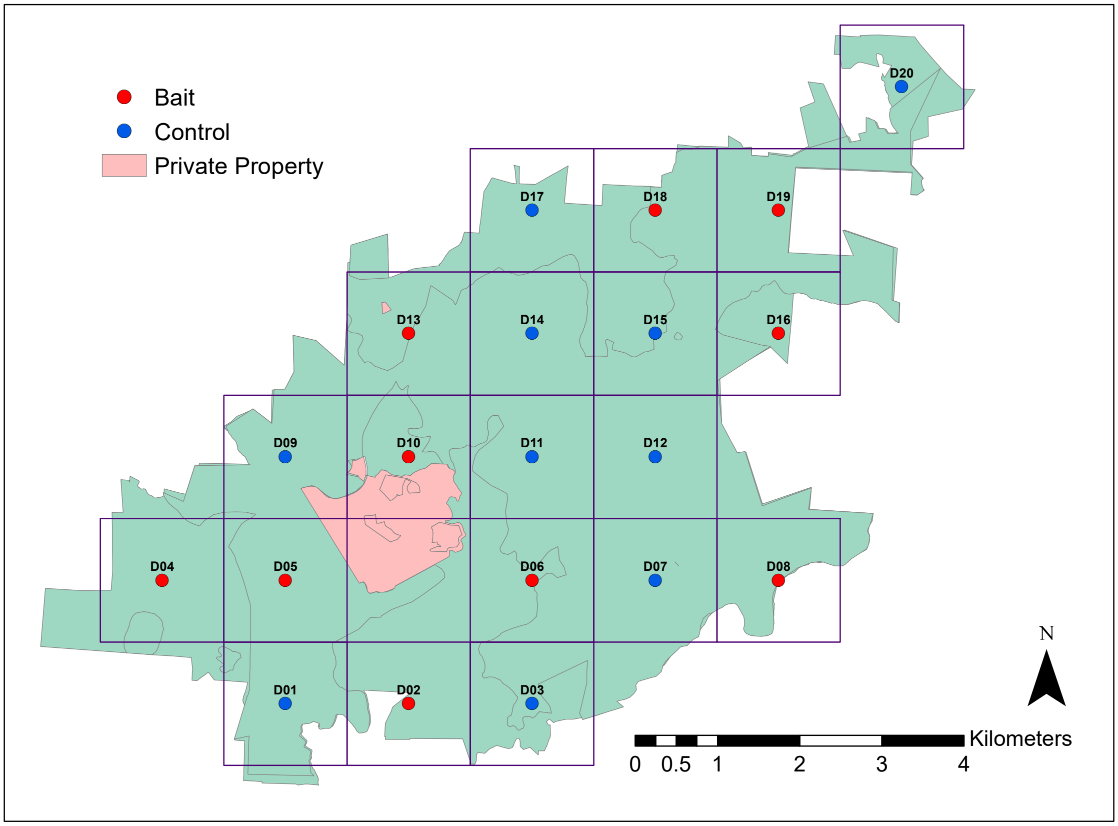

Fig. 2. Map of DuPont State Forest with surveyed camera locations and site identification codes. Baited sites on this map are for the first 6-week sampling period. For second 6-week sampling period, the baited and unbaited sites were switched.

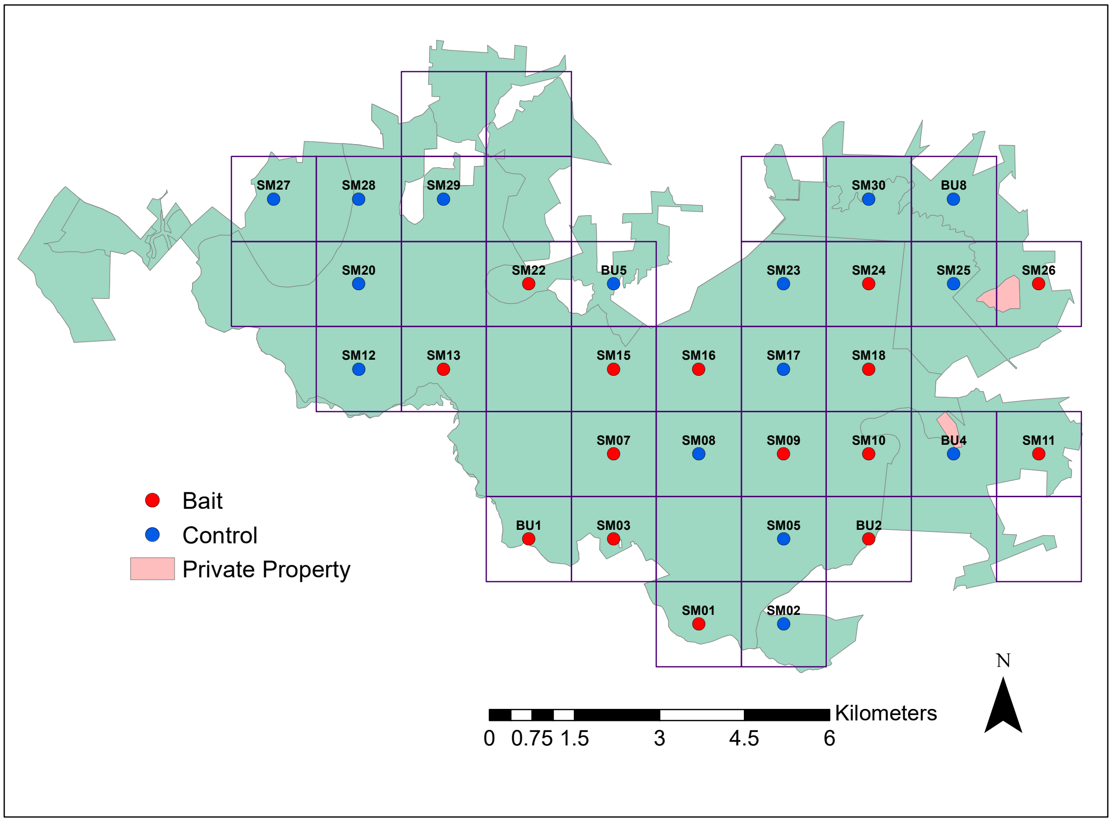

Fig. 3. Map of South Mountains area with surveyed camera locations and site identification codes. Baited sites on this map are for the first 6-week sampling period. For second 6-week sampling period, the baited and unbaited sites were switched.

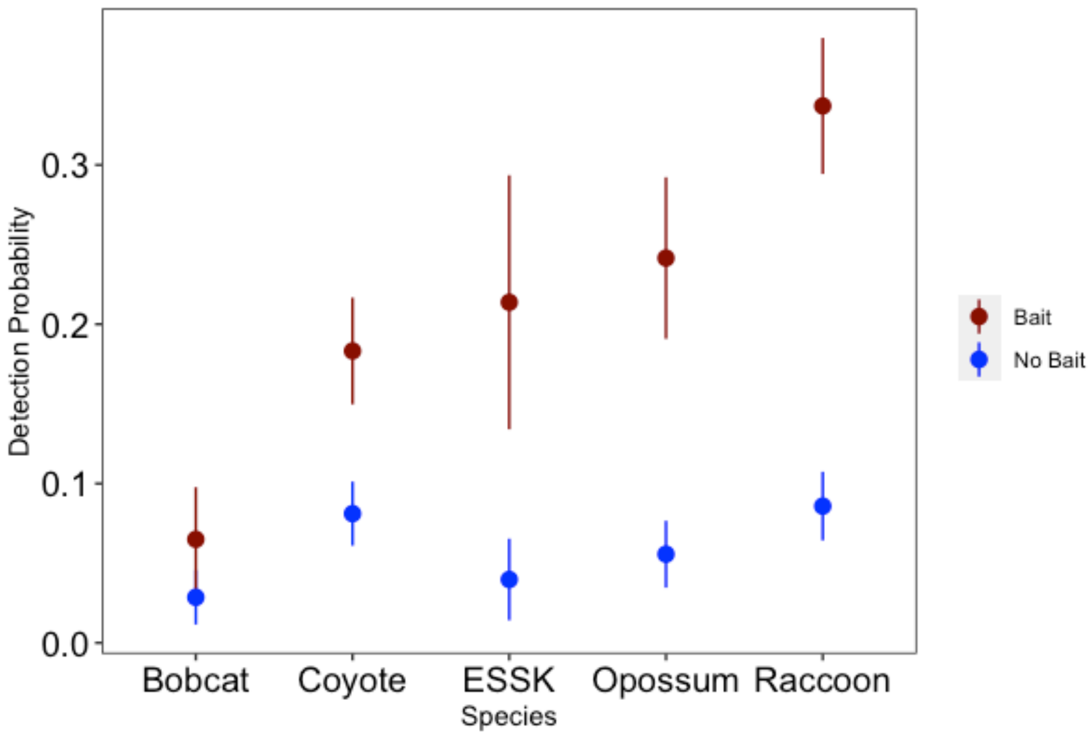

Fig. 4. Effect of bait on detection probability for each species (eastern spotted skunk is abbreviated as ESSK on the x-axis). Striped skunks did not show a response to bait, so data for that species does not appear here. The error bars represent the standard errors for the detection probability not the 95% margin of error.

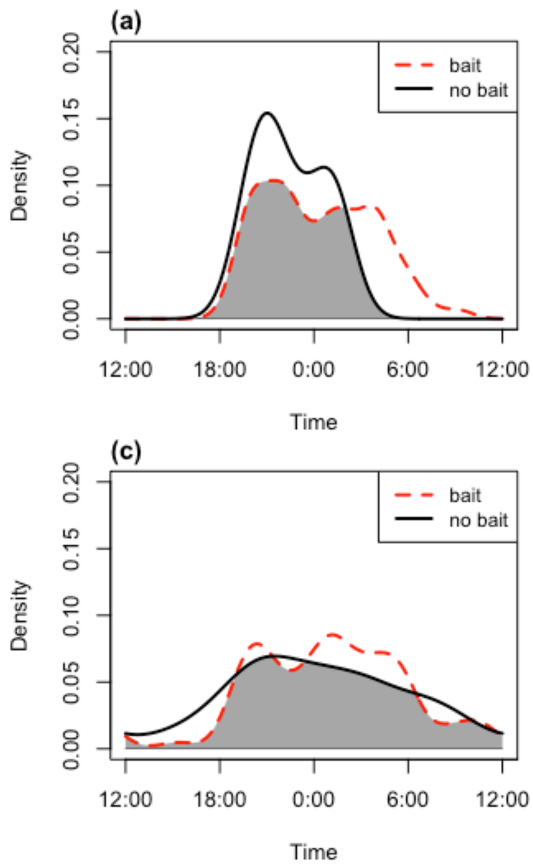

Fig. 5. Temporal activity overlap for raccoon (a), opossum (b), and coyote (c) using kernel density estimates. The time axis is set to 24 hours, so 0:00 represents midnight. The grey area indicates the overlap in temporal activity between baited and unbaited sites. Only raccoons showed a significant difference in activity periods between baited and unbaited sites (W = 0.199, p-value <0.05).

CHAPTER 2

DEN SITE SELECTION OF AN ELUSIVE MESOPREDATOR OF CONSERVATION CONCERN IN NORTH CAROLINA

INTRODUCTION

Spotted skunks, particularly eastern spotted skunks (*Spilogale putorius*), are increasingly of conservation concern (Gompper and Jachowski 2016). There has been a drastic decline in spotted skunk populations range-wide since the 1940s and 1950s, and populations today remain scarce (Gompper 2017). Because of continued eastern spotted skunk decline and lack of basic knowledge, the North Carolina Wildlife Resources Commission (NCWRC), along with several other states, designated the eastern spotted skunk as a priority species or species of greatest conservation need (Gompper and Jachowski 2016, Olfenbuttel 2018).

Gompper (2017) suggests there may be multiple drivers for the spotted skunk's decline rather than one main source. Throughout the 1920s – 1940s, spotted skunks were trapped and harvested heavily for their pelts in the fur trade (Gompper and Hackett 2005). After the 1940s, wildlife managers noticed a decline in spotted skunk harvests; by the early 1950s successful harvests were less than 10% of pre-decline numbers, and by the 1980s, harvests were down to less than 1% of pre-crash numbers (Gompper and Hackett 2005). These lower trapping successes were likely a result of low abundances of spotted skunks. Despite decreased harvesting (and in some places banned spotted skunk trapping) the species has not recovered, suggesting that there might be other drivers for the population declines (Gompper 2017). During this same time period, land conversion for agriculture increased as the agricultural system became more industrialized and the U.S. increased the use of pesticides and insecticides. This agricultural development likely resulted in large quantities of habitat loss, especially for the plains subspecies of the spotted skunk (*S. p. interrupta*). Other potential drivers of the eastern spotted skunk decline include disease (such as canine distemper) and changes in the predator community which influences predation risk and competition (Gompper and Jachowski 2016, Gompper 2017).

Given concerns about habitat loss and inter-specific interactions, understanding fine-scale habitat selection is important for management and recovery of spotted skunks (Eng and Jachowski 2019). Small carnivores like the spotted skunk are relatively short lived and produce only a single litter of offspring each year, making it critically important that adults survive to successfully produce offspring each year of their life (Harris and Ogan 1997, Olfenbuttel 2018). Den sites—defined as secure structures that are used for rest, sleep, or reproduction (Robitaille et al. 2020)—offer shelter from predators and weather, and they offer a safe place for female skunks to give birth and rear kits (Hossler et al. 1994, Arjo et al. 2003). Therefore, understanding where eastern spotted skunks, especially females, choose to den is important for their recovery.

Den site selection in spotted skunks is highly variable and there are multiple explanations for what best determines these used sites. Eastern spotted skunks tend to be associated with dense understory and a complex forest structure (Lesmeister 2007, Lesmeister et al. 2009). They have been found at den sites in ground burrows or root systems (Lesmeister et al. 2008, Sprayberry and Edelman 2018, Eng and Jachowski 2019) and in tree cavities (Crabb 1948, Doty and Dowler 2006). Some researchers suggest that thermoregulation (Crabb 1948, Lesmeister et al. 2008, Eng and Jachowski 2019) and food resource availability (Crabb 1948, Sprayberry and Edelman 2016, Eng and Jachowski 2019) are factors important in skunk den site selection. Moreover, there are hypotheses suggesting that cover from predators (Lesmeister 2007, Sprayberry and Edelman 2018) and interspecific competition (Jones et al. 2008, Harris et al. 2020) are influential in den site selection. Roemer et al. (2002) and Jones et al. (2008) discuss how high competition and frequent interactions with predators or other small carnivores may lead to spotted skunk behavioral adaptations in resource use, including den site selection.

In this study our objective was to assess how fine-scale habitat characteristics influence spotted skunk den site selection in North Carolina. We hypothesized that shelter from weather and cover from predation were important for den site selection, so we predicted that selection would be positively associated with dense forest structure (Fedriani and Fuller 2000, Lesmeister et al. 2010). We further hypothesized that foraging accessibility and travel corridors (Sprayberry and Edelman 2016, Eng and Jachowski 2019), reduced predator maneuverability (Eng and Jachowski 2019), and den type (Sprayberry and Edelman 2018, Harris et al. 2020) were important for determining den site selection (Table 1). Results from this study provide information into what types of site-specific habitat managers should promote to increase resource availability for eastern spotted skunks.

METHODS

Study Area

From January to August 2018 through 2020, we focused our eastern spotted skunk den site selection study in two areas of North Carolina (DuPont State Recreational Forest and South Mountains State Park with the surrounding Foothills Conservancy) known to contain sightings of eastern spotted skunks. DuPont State Recreational Forest and the South Mountains area are located in the Blue Ridge region of the Appalachian Mountains (See Figure 1 from Chapter 1). DuPont ranges from about 701 to 1097 m (2300-3600 ft) in elevation and South Mountains ranges up to 914 m (3000 ft). Both areas primarily consist of mixed deciduous forests with some evergreen species including Mountain Laurel (*Kalmia latifolia*) and Rhododendron (*Rhododendron spp.*). During our study, DuPont had a monthly average temperature range from 0.7°C to 19.3°C, 3.1°C to 19.3°C, and 5.3°C to 15.2°C in 2018, 2019, and 2020 respectively (National Centers for Environmental Information, https://www.ncdc.noaa.gov/). South Mountains area monthly average temperature ranged from 0.9°C to 21.2°C, 4.2°C to 21.1°C, and 6.2°C to

16.3°C in 2018, 2019, and 2020 respectively. The monthly total precipitation for DuPont area ranged from 8 cm to more than 25 cm in both 2018 and 2019 and ranged from 10 cm to more than 25 cm in 2020. South Mountains had a monthly precipitation ranging from 5 cm to more than 25 cm in both 2018 and 2019, and it ranged from 5 cm to 20 cm in 2020 (National Centers for Environmental Information, https://www.ncdc.noaa.gov/).

Field Data Collection

We captured, collared, and radio-tracked eastern spotted skunks to identify den sites (Figure 1). To trap skunks, we chose locations where they had been spotted previously on game cameras or chose locations by stream drainages with dense understory vegetation where past research suggested we would be more likely to encounter spotted skunks (Lesmeister 2007, Eng and Jachowski 2019). We trapped skunks from January through May 2018-2020 and began radio-tracking collared skunks after a full day (24+ hours) since capture. We used squirrel-sized (48.26 cm x 15.24 cm x 15.24 cm) Tomahawk live traps (Tomahawk Live Trap, Pro Series Model 103SS, Hazelton, Wisconsin) baited with canned cat food, and we organized the traps in lines or clusters containing one to four traps. When we caught a healthy adult skunk, we fitted the skunk with one of two types of very high frequency (VHF) radio-collars weighing approximately 16 grams: zip-tie collars (model M1545) and neoprene collars (model M1740; Advanced Telemetry Systems, Isanti, MN, USA). We collared a skunk only when the collar represented less than five percent of its body weight following the American Society of Mammalogists guidelines (Wilson et al. 1996, Sikes et al. 2016). Thus, we did not collar skunks under 320 grams. In addition to collaring a captured skunk, we determined sex and age based on body size and tooth wear (Lesmeister 2007), weighed it on its initial capture, ear-tagged both ears (model 1005-1L1; National Band and Tag Company, Newport, KY, USA), inserted a PIT-tag, checked body condition, collected hair samples, and collected ectoparasites if present. For all skunk trapping, processing, collaring, and radio-tracking, we followed American Society of Mammalogists guidelines (Sikes et al. 2016) and complied with Clemson University Animal Care and Use Committee protocol (Permit: AR 2017-065).

We tracked each collared skunk during daylight hours 1-3 times per week (Lesmeister et al. 2008, Sprayberry and Edelman 2018). We used a 3-element yagi antenna to find and navigate toward the skunk in its den. For every den site, we determined two paired random locations representing available den sites. The first random point (RA) was a potential den site located between 50 m and 150 m away from the used den site. The second random point (RB) was an available den site located between 150 m to 250 m away from the used den site (Doty and Dowler 2006). Thus, availability was defined as the area within a radius of 250 m from the used den site. We looked for each putative (available) den site along each of two randomly generated bearings. We characterized available dens as sites with at least one entrance that had around 10 cm x 10 cm diameter, sites that excluded sunlight during the day (e.g. burrow cavity and not only an overhanging structure), and sites that provided shelter from the elements and predators (Crabb 1948). We completed habitat surveys at the used site and both available den sites. Den site observations at the same location were considered independent observations if the den was used at least five days apart (Eng and Jachowski 2019). For these replicate points, we completed habitat surveys at two new available den sites but did not resurvey at the used site. If the same site was reused greater than one month apart, we surveyed at the used site and two new random sites.

At each used and available den site, we established a 10 m x10 m plot centered on the den site or available site (Figure 2). Using a 50 cm x 25 cm Daubenmire frame, we estimated the percent of various types of ground cover (e.g. forbs and grasses) at the end of each node (North, South, East, West) and at the center of the plot. At the plot center, we measured canopy closure with a Nikon DSLR camera and fisheye lens on auto-exposure settings held at breast height. To estimate understory, we counted the number of Rhododendron, mountain laurel, and other woody stems ≥0.7cm in diameter and counted course woody debris (CWD) ≥10 cm in diameter along each 5 m x 1 m transect. We measured the basal area with a 10-factor Cruz-All gauge while standing at the center of the plot. We recorded the type of den, entrance orientation, entrance size, and slope (Tables 2a-b, Figure 3). We transformed the circular degree measure of orientation to a linear measure in which the SE and NW directions were represented by a value of 0 and 180 respectively (Eng and Jachowski 2019). The NE and SW directions were not differentiated with this transformation (i.e. a value of 90 represented either direction). When the orientation measured between 0°–314.9°, we used the equation conversion = |orient° – 315°|, and when the orientation measured ≥315°, we used the equation conversion = |orient° – 495°| to calculate orientation as a linear measure. To calculate distance to nearest stream or drainage channel we used ArcGIS 10.6.1 (Esri 2018) and hydrography flowlines data (NC Streams Mapping Program 2021 https://www.nconemap.gov/pages/streams).

Analysis

We developed 19 *a priori* models to examine the relative support for several local factors we hypothesized would influence spotted skunk den site selection (Table 1). Firstly, we hypothesized that habitat characteristics that reduce predation risk would be strong indicators of eastern spotted skunk den site selection. Lesmeister et al. (2010) found that eastern spotted skunks were predated upon by avian species and ground mammal species, so aerial cover and understory cover would be important for reducing predation risk (Lesmeister et al. 2008, Eng and Jachowski 2019). We predicted that skunks would select den sites in locations with more overstory and understory cover. In addition to cover, we predicted that skunks would select for sites on steeper slopes reducing predator mobility (Litvaitis et al. 1985, Lesmeister et al. 2008). For our shelter hypothesis, we predicted that southeast-facing dens were more likely to be selected because south-facing entrances should help keep the dens warm (Kinlaw 1995, Eng and Jachowski 2019). These sites would have smaller entrances for protection from weather (Lesmeister et al. 2008) and to keep the temperature stable in the den. Furthermore, we hypothesized that features related to foraging potential and travel accessibility would be important for den site selection. We predicted a positive relationship between the likelihood of den site selection and forbs and grasses, CWD, and snags because these features likely contain abundant prey for the spotted skunk (Loeb 1999, Sprayberry and Edelman 2016). We predicted a negative relationship of den site selection with distance to nearest drainage or stream channel because this landscape feature could act as a travel corridor and possible foraging location (Eng and Jachowski 2019). We hypothesized that den type is important for den site selection (Harris et al. 2020) in which we predicted that eastern spotted skunks were more likely to select den sites in ground burrows or root systems than in rock substrate.

To evaluate support for our *a priori* hypotheses, we used an information theoretic AICc model selection approach in a discrete choice framework using program R (version 4.0.3; R Core Team 2020, Vienna, Austria). We created the discrete choice models using R package "mlogit" (Croissant 2020). Because of differences found in den site selection between male and female spotted skunks (Eng and Jachowski 2019, Harris et al. 2020), we hypothesized that males would select sites differently than females. To compare the effects of sex on *S. putorius* rest selection, we ran the model selection for males and for females separately. We scaled and centered our quantitative covariates with a mean of zero and standard deviation of 1 for each dataset. We selected our top model sets using the 95% confidence set rule (Burnham and Anderson 2002, Symonds and Moussalli 2011), and we defined important covariates in which the 95% confidence intervals did not overlap zero.

Because there is no null model for discrete choice framework, we evaluated the predictive performance of our top models using 10 iterations of k-fold cross validations (Boyce et al. 2002). We used testing sets created from randomly selecting 20% of our data (maintaining the 1:2 ratio of used to available) and used the remaining 80% of our data as the training set (Bodinof et al. 2012, Harris et al. 2020). Using the results from 10 iterations on our top models for each dataset, we calculated the proportion of correct predictions (i.e. when the model correctly predicted the used site). Proportion of 0.5 (i.e. 50%) indicates that the model did not perform better than random chance, and a proportion of 1.0 (i.e. 100%) indicates perfect performance.

RESULTS

We recorded data for a total of 273 skunk den sites (175 dens for males, and 98 dens for females) from 30 spotted skunk individuals (24 males and 6 females; Table 3). The mean number of used den sites for each male individual was 7.29 (range = 1-37), and the mean number of used dens for each female individual was 16.33 (range = 3-31). We found that skunks used previously occupied den sites 47 times (23 reuses for males and 24 reuses for females). We observed only five instances where reused den sites were by different individuals; the rest of reused sites were by the same individuals. We observed 20 locations in which the same individual used sites consecutively (i.e. within 7 days of last use) and sometimes more than twice in a row (range = 2-5 times in a row). The majority of consecutive reuses were by females; however, there was on male in DuPont that had six instances of consecutive den site reuse. There was one instance of communal denning by a male and female on 25 March 2018. We observed skunks denning in ground burrows (45.42%), in rocky outcrops (24.18%), and in root systems and tree-related sites (30.40%). One individual used a tire one time as a denning location, but because we had no "other" den site categories we excluded this den location from our analysis. One female used a tree cavity with a very large basal opening (entrance size = 7200 cm^2). We considered this an outlier and excluded this den site from our analysis.

Males

There was model selection uncertainty for males with the global model and a subglobal model accounting for over 95% of the model weights and each were similar in model weight (Table 4). Because the second-best model (our global model) added a covariate with a 95% confidence interval that did not overlap zero, we chose the global model as our top model. For this top model, six of the covariates (basal area, canopy closure, distance to stream or channel, entrance size, and forbs and grasses) had 95% confidence intervals that did not overlap zero (Table 5). Male den site selection was negatively associated with basal area, distance to stream channel, and percent of ground covered by forbs and grasses. The odds of selection decreased 33% for every 10.22 m^2/acre (110 ft^2/acre) increase in basal area (Figure 4). The odds of a male selecting a site decreased 56% with every 100-meter increase in distance to a stream channel (Figure 5a), and there was a 32% decrease in odds of den selection for every 10% increase in forb and grass ground cover (Figure 5b). Male den sites were positively associated with canopy closure, entrance size, and slope. The odds of a male skunk selecting a den site increased 19.4% with every 20% increase in canopy closure (Figure 5c). The odds of selection increased 7.65% with every 100 cm^2 increase in the den entrance size (Figure 5d), and there was a 52% increase in the odds of selection for every 34% increase in slope (Figure 5e). The global model correctly predicted male den site use 57% of the time.

Females

There was model selection uncertainty for females with five models making up the 95% confidence set. However, the forest structure with den type model and a subglobal model were the top two models in the female dataset making up 73% of the model weights (Table 6), so we focused on those top two models. Because the second-best model (the subglobal model) did not add covariates with 95% confidence intervals that did not overlap zero, we kept the forest structure and den type model as our top model. For this top model, only basal area and den type had 95% confidence intervals that did not overlap zero (Table 7). Relative to rocky outcrop substrate, female den site selection was negatively associated with root system den types, and selection was negatively associated with basal area. The odds of a female selecting root system den types were 22% less relative to rocky outcrop sites, and the odds of selection decreased 51% for every 10.22 m^2/acre (110 ft^2/acre) increase in basal area (Figure 4). The top model for female skunks correctly predicted den site use 50% of the time.

DISCUSSION

Our results suggest that eastern spotted skunk den site selection is highly variable, and there was support for the hypothesized influence of predation risk, foraging availability, ease of travel, and den type on den site selection. While validation results of our top models for both sexes suggested poor predictive performance for identifying used from randomly available den sites (for which there are several potential explanations discussed below), we believe there remain several biologically important features we found to be associated with used den sites, and these features are supported in other studies of this species. The effect of vegetative cover on male and female den site selection is supported by results from Lesmeister et al. (2008), Sprayberry and Edelman (2018), and Eng and Jachowski (2019) in which skunks used dense vegetation likely to hide from predators. Moreover, our finding that male den site selection was likely associated with steeper slopes and close proximity to drainage channels has similarly been observed in other areas (Lesmeister et al. 2008, Eng and Jachowski 2019) suggesting male den site selection was associated with features related to foraging and travel. Further, only female skunk den site selection appeared to be associated with den type (Harris et al. 2020).

Of the several important fine-scale habitat characteristics, attributes related to predation risk made up the most supported covariates. Den site selection had a negative relationship with basal area and a positive relationship with canopy closure. A high basal area in our study areas typically indicated sites with a lot of medium-sized trees rather than a few very large trees. Because the canopy closure photos were taken at breast height, the photos encapsulated understory with overstory canopy. Therefore, high canopy closure typically indicated cover from a dense understory or a combination of overstory and understory canopies. Lesmeister et al. (2010) found that the primary predator of spotted skunks are avian predators such as the great horned owl (*Bubo virginianus*). Thus, selecting for den sites in a closed understory could protect and hide spotted skunks from avian predators. In addition to predator avoidance, dense vegetative cover may have thermoregulation benefits (De Frenne et al. 2019). Lastly, eastern spotted skunks are considered agile and good climbers (Kinlaw 1995, Olfenbuttel 2018). Therefore, the positive association with slope might allow for a quick an easy escape up or down steep terrain to the safety of a den while reducing the mobility of larger and less agile ground predators.

In addition to cover from predators, access to areas with forage and ease of travel appear to be important for male den site selection (Eng and Jachowski et al. 2019). Drainage channels make up a vast majority of stream networks (Montgomery and Buffington 1997, Hansen 2001), and Eng and Jachowski (2019) hypothesized that they could be a travel network and might have higher availability of potential food resources. These mesic areas likely have higher prey diversity and abundances including salamanders and snakes, which have been documented in spotted skunk diets (Sprayberry and Edelman 206, Thorne et al. 2017). However, drainage channels could be risky areas because other carnivores and spotted skunks likely use these travel corridors (Dijak and Thompson III 2000, Rodriguez et al. 2020, Breault et al. 2021). Thus, selection for drainage channels by males, but no support for an effect in females, could suggest that these areas are too risky for rearing kits. Contrary to what we expected, male den site selection was negatively associated with forb and grass ground cover. This effect is likely not related to foraging but rather to an open understory in which more sunlight reaches the ground and there is less competition for soil nutrients (Knapp et al. 2014). Because of this possible relationship in which more forbs and grasses would be present with an open understory, skunks would likely avoid areas with a lot of forb and grass ground cover (Perry et al. 2018).

In contrast to our prediction and Lesmeister et al. (2008), male spotted skunks appeared to use den sites with larger entrance sizes. This result is likely because the rocky outcrop den sites had the largest entrance sizes with exception to one very large tree cavity. Thus, the low availability of rocky outcrop sites—and hence low availability of sites with large entrances—likely resulted in males appearing to select for those larger openings. Moreover, to define an available den site, we used a relatively small entrance size which would further reduce the availability of large entrances despite the occasional use of den sites with larger openings. Although female den site selection was not affected by entrance size, the rocky outcrop substrate appeared to be an important factor for female eastern spotted skunks (22.68% of used female dens and 14.43% of available female dens). Females may be pickier than males about the den type because they are looking for sites that are suitable for parturition and rearing kits. Rocky outcrop dens could provide additional protection from ground predators attempting to excavate dens (Sprayberry and Edelman 2018).

We collected one of the highest numbers of den sites ever reported for this species, but our model validation results indicated that our top model for males and females were still poor at predicting used den sites. This result might show that spotted skunks could be generalists or opportunistic in selecting dens. On the other hand, there are several sampling and analytical reasons why our validation results were so poor. First, our analysis was limited in that we could not partition our data to analyze the study areas independently. Thus, variation between the study areas (populations) might have contributed to poor model performance. In addition, our sample size did not allow us to further split up female data into litter-rearing females and non-litter-rearing females. Harris et al. (2020) found that females during the litter-rearing season selected den sites differently than males and females outside of the litter-rearing season. Given that several explanations for differences between female and male spotted skunk den site selection tend to be related to the female's reproductive ability, we recommend investigations into den selection during rearing season. Second, there seemed to be few differences in variation in our fine scale measurements between used dens and available dens. Thus, we were easily able to find available den sites similar to used den sites within our defined available area (radius of 250 m) that may have made assessing selection difficult. Third, given the support for covariates related to predation risk, directly estimating predator activity likely would be a better predictor of eastern spotted skunk den site selection. However, estimating raptor activity is difficult (Andersen 2007, Vali et al. 2018). We attempted to estimate interspecific competition from the mesopredator (e.g. coyote, bobcat, fox, striped skunk, opossum, and racoon) relative activity data from the baited-unbaited remote camera array project (see Chapter 1), but we had trouble fitting strong landscape models of relative activity for our competitor and predator species to include in this den selection study. Therefore, we encourage future researchers to pair studies of spotted skunks with dedicated studies of their predators to be able to directly assess the effect of predation or competition on eastern spotted skunk den site selection.

Understanding how fine-scale features affect den site selection has important management implications and could aid in the recovery of the species. Forest structure was likely an important aspect for both male and female den site selection, so site-specific management practices promoting a complex understory with vegetative cover and closure would be beneficial for this species. Because male spotted skunks appeared to select for areas with steep slopes and drainage channels, we encourage managers to particularly consider managing forest sites containing steep slopes near streams or channels. More broadly, the consistent use of dens almost exclusively within both study areas indicates the importance of these protected forest habitats for eastern spotted skunks. Further research is needed to understand the extent to which spotted skunks persist, including their den site selection patterns, outside of relatively unfragmented protected forests. Regardless, our findings support research on this species from other protected forest environments and collectively suggest that site-specific maintenance of forests with low basal area and dense understory cover is important for the conservation and restoration of spotted skunks in the Southern Appalachian region.

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TABLES

Table 1. Hypotheses table for male and female spotted skunk den site selection. In the predictions column, the "+" and "-" indicates whether the covariate is positively or negatively related to den site selection. For the case of categorical variables "+" indicates a positive difference from the reference category and "-" indicates a negative difference from the reference category for probability of den site selected.

Hypotheses	Predictions	Literature
1. Understory only	Woody stems: +	Perry et al. 2018
2. Overstory only	Canopy closure: + Basal area: +	Lesmeister et al. 2008, Lesmeister et al. 2010, Perry et al. 2018, Eng and Jachowski 2019
3. Forest structure (over and understory)	Canopy closure: + Basal area: + Woody stems: +	Lesmeister et al. 2010, Perry et al. 2018, Sprayberry and Edelman 2018, Eng and Jachowski 2019
4. Shelter from weather	Entrance size: - Orientation: -	Lesmeister et al. 2009
5. Topographic	Slope: +	Litvaitis et al. 1985 Lesmeister et al. 2008
6. Travel	Dist stream: -	
7. Foraging potential	%Forbs&grasses: + CWD: + Snags: + Dist stream: -	Crabb 1948, Loeb 1999, Sprayberry and Edelman 2016, Eng and Jachowski 2019
8. Den type	Den type (categories): ground burrow +, rocky outcrop (reference), root system +	Harris et al. 2020
9. Overstory and travel	Canopy closure: + Basal area: + Dist stream: -	

10. Forest structure (over and understory) and travel	Canopy closure: + Basal area: + Woody stems: + Dist stream: -	Sprayberry and Edelman 2018, Eng and Jachowski 2019
11. Forest structure (over and understory) and den type	Canopy closure: + Basal area: + Woody stems: + Den type (categories): ground burrow +, rocky outcrop (reference), root system +	
12. Travel and shelter	Entrance size: - Orientation: - Dist stream: -	
13. Forest structure (over and understory) and foraging	Canopy closure: + Basal area: + Woody stems: + CWD: + %Forbs&grasses: + Snags: + Dist stream: -	
14. Foraging and den type	%Forbs&grasses: + CWD: + Snags: + Dist stream: - Den type (categories): ground burrow +, rocky outcrop (reference), root system +	
15. Subglobal (shelter, foraging, topographic)	Orientation: - Entrance size: - %Forbs&grasses: + CWD: + Snags: + Dist stream: - Slope: +	Lesmeister et al. 2008, Lesmeister et al. 2009
16. Subglobal (topographic, den type, forest structure)	Canopy closure: + Basal area: + Woody stems: + Slope: + Den type (categories): ground burrow +, rocky outcrop (reference), root system +	

17. Subglobal (travel, topographic, forest structure, shelter)	Canopy closure: + Basal area: + Woody stems: + Dist stream: - Slope: + Orientation: - Entrance size: -
18. Subglobal (forest structure, travel, den type, shelter)	Canopy closure: + Basal area: + Woody stems: + Dist stream: - Orientation: - Entrance size: - Den type (categories): ground burrow +, rocky outcrop (reference), root system +
19. Global	Canopy closure: + Basal area: + Woody stems: + Dist stream: - CWD: + %Forbs&grasses: + Snags: + Entrance size: - Slope: + Orientation: - Den type (categories): ground burrow +, rocky outcrop (reference), root system +

Table 2. Den site and habitat covariates measured for each used and available eastern spotted skunk den site (a), and the average of values (with the range in parentheses) of those covariates at used dens and available dens for each sex (b).

(a)

Covariate	Description
Orientation	Direction that the entrance of the den site faces, measured as degrees from southeast (0-180°, SE-NW)
Slope	Percent slope at the den site where the topographic slope was steepest; used clinometer
Entrance size	Calculated area of den site entrance opening from measured entrance largest width and largest height (cm^2)
Den type	Categorical classification for the type of den site or putative den site (ground burrow, rocky outcrop, and root system; hollow logs and tree cavities were included in the root system category).
Snags	Number of standing snags in the habitat survey plot
Basal area	Calculated from number of "in" trees using 10-factor gauge (m^2/acre)
Percent forbs and grasses	Percent of ground in Daubenmire frame covered by grasses and forbs
Canopy closure	Percent of canopy closed estimated from photo taken with fisheye lens at center of survey plot
Woody stems	Averaged total number of all standing woody stems that were ≥0.7 cm in diameter; counted for each transect
CWD	Averaged number of downed coarse woody debris that were ≥10 cm wide at their midpoint; counted along each transect
Dist stream	Distance (m) to nearest stream or drainage channel

(b)

	Males		Females	
Covariate	Used dens	Available dens	Used dens	Available dens
Orientation (º)	100.20 (1-179)	92.84 (0-179)	81.27 (2-171)	82.08 (2-180)
Slope (%)	23.79 (0-92)	18.84 (0-68)	20.34 (0-68)	18.12 (0-58)
Entrance size (cm^2)	336.98 (28-5460)	185.90 (20-1920)	264.20 (32-3168)	166.30 (25-4480)
Snags	1.00 (0-8)	1.04 (0-8)	1.25 (0-14)	1.17 (0-9)
Basal Area (m^2/acre)	6.78 (0.93-17.65)	7.95 (1.86-20.44)	6.21 (0.00-12.08)	7.77 (0.93-18.58)
Forbs and grasses (%)	2.84 (0-41)	4.32 (0-44)	3.65 (0-19)	3.73 (0-26)
Canopy closure (%)	85.19 (14.0-99.7)	78.36 (12.6-99.6)	90.46 (55.5-99.8)	88.87 (49.4-99.7)
Woody stems	7.78 (0.25-47.00)	6.00 (0.00-74.25)	5.71 (0.25-31.75)	5.81 (0.00-22.75)
CWD	0.50 (0.00-4.50)	0.57 (0.00-3.50)	0.50 (0.00-3.00)	0.48 (0.00-2.25)
Distance drain (m)	44.21 (0.04-201.46)	62.25 (0.25-214.58)	53.23 (2.58-169.59)	59.02 (0.30-193.85)

Table 3. The number of den sites used and the dates we tracked each spotted skunk. "SM" represents the South Mountains area and "DP" represents the DuPont area. The dates in the "Period Tacked" column are represented by day/month/year. The first date indicates the first day we tracked the skunk and end date indicates the last day we tracked the skunk.

Skunk ID	Sex	Sites	Study Area	Period Tracked
F1	F	14	SM	03/18/2018-07/15/2018
F2	F	20	SM	03/18/2018-08/12/2018
F3	F	31	SM	04/22/2019-08/30/2019, 02/03/2020-05/18/2020
F5	F	3	SM	02/25/2020-03/11/2020
F6	F	25	SM	04/20/2020-07/31/2020
S4	F	5	DP	05/20/2019-07/08/2019
M1	M	4	SM	02/24/2018-03/25/2018
M11	M	6	SM	05/21/2018-08/09/2018
M13	M	5	SM	05/11/2018-08/09/2018
M14	M	2	SM	03/19/2019-03/25/2019
M15	M	2	SM	03/13/2019-03/24/2019
M17	M	13	SM	04/25/2019-08/30/2019
M18	M	25	SM	03/24/2019-06/27/2019, 02/27/2020-07/28/2020
M19	M	7	SM	03/23/2019-05/30/2019
M2	M	1	SM	02/24/2018
M20	M	2	SM	06/01/2020-06/08/2020
M22	M	5	SM	04/20/2020-06/08/2020
M24	M	2	SM	02/03/2020-03/30/2020
M26	M	4	SM	02/27/2020-03/30/2020
M27	M	8	SM	03/27/2020-06/22/2020
M3	M	1	SM	03/25/2018
M4	M	15	SM	05/23/2018-06/28/2018, 01/02/2019-05/30/2019
M8	M	2	SM	04/26/2018, 12/31/2018
S1	M	12	DP	04/27/2019-08/13/2019
S10	M	5	DP	04/07/2020-05/05/2020
S2	M	2	DP	04/27/2019-06/18/2019
S3	M	37	DP	05/15/2019-08/31/2019, 02/17/2020-04/20/2020
S5	M	4	DP	02/14/2020-02/19/2020
S6	M	10	DP	03/17/2020-04/21/2020
S9	M	1	DP	04/06/2020

Table 4. AICc table of male spotted skunk den site selection. Model numbers correspond with numbers in Table 1.

Model	Log-Likelihood	AICc	Δ AICc	K	weight
Subglobal 17	-147.63	309.94	0.00	7	0.518
[a]Global	-142.11	310.15	0.21	12	0.467

[a]Model used in validation and for prediction graphs

Table 5. Coefficients and 95% confidence intervals of the top model (Global model) for males. Covariates with "*" indicate 95% confidence intervals did not overlap zero. The "OR" column contains the calculated odds ratios.

Covariate	Estimate	SE	Lower CI	Upper CI	OR
*Basal area	-0.40	0.13	-0.67	-0.14	0.670
*Canopy closure	0.68	0.24	0.20	1.15	1.968
CWD	-0.04	0.13	-0.29	0.21	0.960
*Distance to stream	-0.81	0.19	-1.19	-0.44	0.443
*Entrance size	0.45	0.18	0.10	0.81	1.571
*Forbs	-0.38	0.14	-0.66	-0.10	0.684
Ground burrow	0.19	0.33	-0.46	0.84	1.210
Orientation	0.05	0.11	-0.17	0.27	1.049
Root system	-0.25	0.33	-0.90	0.41	0.782
*Slope	0.42	0.16	0.11	0.73	1.522
Snags	0.13	0.13	-0.12	0.39	1.141
Woody stems	0.22	0.15	-0.06	0.51	1.250

Table 6. AICc table of female spotted skunk den site selection. Model numbers correspond with numbers in Table 1.

Model	Log-Likelihood	AICc	Δ AICc	K	weight
[a]Forest structure + Den type	-90.76	192.18	0.00	5	0.396
Subglobal 16	-89.79	192.52	0.34	6	0.333
Overstory	-95.50	195.13	2.95	2	0.091
Subglobal 18	-88.86	195.36	3.18	8	0.081
Overstory + travel	-95.31	196.89	4.71	3	0.037

[a]Model used for validation and prediction graphs

Table 7. Coefficients and 95% confidence intervals of the top model (model 11) for females. Covariates with "*" indicate 95% confidence intervals did not overlap zero. The "OR" column contains the calculated odds ratios.

Covariate	Estimate	SE	Lower CI	Upper CI	OR
*Basal area	-0.71	0.18	-1.06	-0.36	0.492
Canopy closure	0.32	0.20	-0.07	0.71	1.372
Ground burrow	-0.58	0.40	-1.37	0.21	0.561
*Root system	-1.31	0.47	-2.23	-0.38	0.271
Woody stems	0.05	0.16	-0.27	0.36	1.049

FIGURES

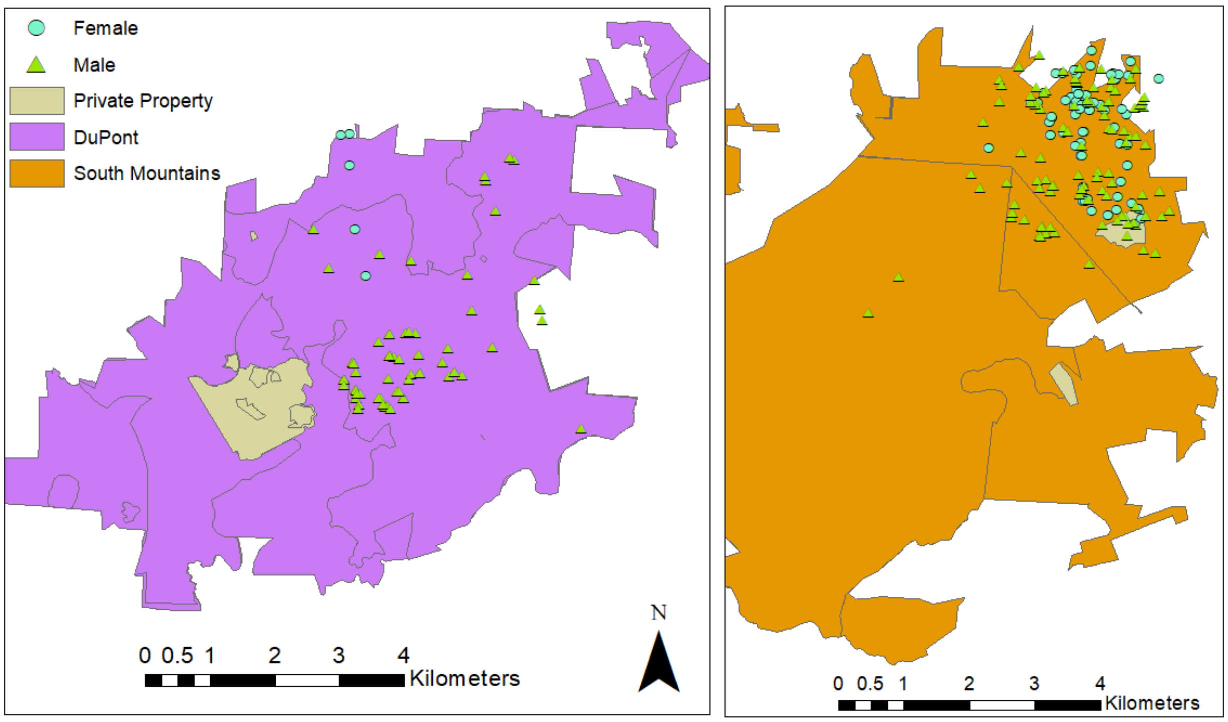


Fig. 1. Spotted skunk used den site locations in DuPont (left) and South Mountains (right) study areas. Spotted skunks tracked in the South Mountains area nearly all occurred in the northeastern part of the park, so only that section of the park is displayed here.

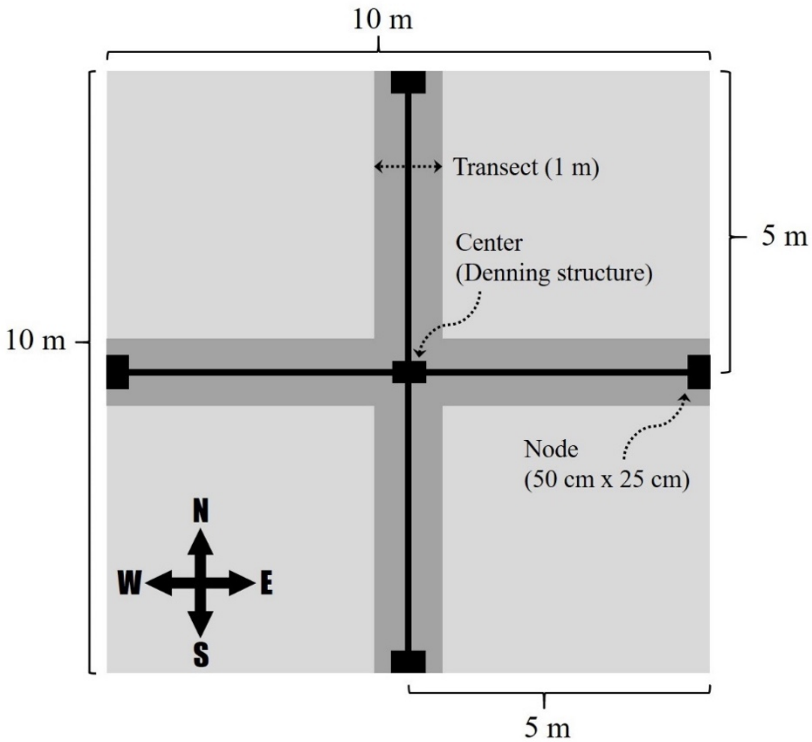


Fig. 2. Diagram of the habitat survey plot at each tracked den site and putative den site. Each black rectangle represents the locations at which we surveyed with the Daubenmire frame. Each black line connecting the nodes to the center are the transects we surveyed.

Eastern Spotted Skunk Habitat/Vegetation Survey - Clemson University

Observer(s): ________________ Skunk ID/Name: __________ UTM E (*x*): _______________

Date surveyed: ______________ Property: _______________ UTM N (*y*): ______________

Date site occupied: ___________ Previously used site: Yes No

Site Characteristics

Survey site:	>50 m >150 m
Den	Bearing: ______

Den type: ground burrow hollow log rocky outcrop root system tree cavity woodrat nest other______________________

# of den entrances: _______
Den orientation (°): _______
Slope at den (%): _______
Aspect at den (°): _______
Entrance size - *diameter at widest* : _____(w) x _____(h)

If tree cavity :
Tree species: ______________
Snag: Yes No
Entrance height (cm): ________

PLOT MEASUREMENTS

Basal area (10 BAF): ______
Canopy type: Mixed Deciduous Coniferous Open
snags in plot: _______

Dominant understory species:
Rhododendron mountain laurel
other_________________ none

***CWD = coarse woody debris (≥ 10 cm diameter)**

NODES	**% Ground Cover (Daubenmire frame)**				
Type	**Center**	**North**	**East**	**South**	**West**
Forb					
Litter					
Rock/Bare					
Grass					
CWD					
Canopy photo #					

TRANSECTS	**Cardinal Direction (within 1 m of transect)**			
Type	**North**	**East**	**South**	**West**
# rocks (≥10 cm - 1 m)				
# boulders (> 1 m)				
# Rhododendron stems				
# mountain laurel stems				
# vines/briers				
# CWD				

Datasheet photo: Yes No ***WRITE COMMENTS ON BACK***

Entered by: ______________ Proofed by: ______________
Date: __________ Date: __________

Fig. 3. Den site datasheet to record measures of den and habitat characteristics.

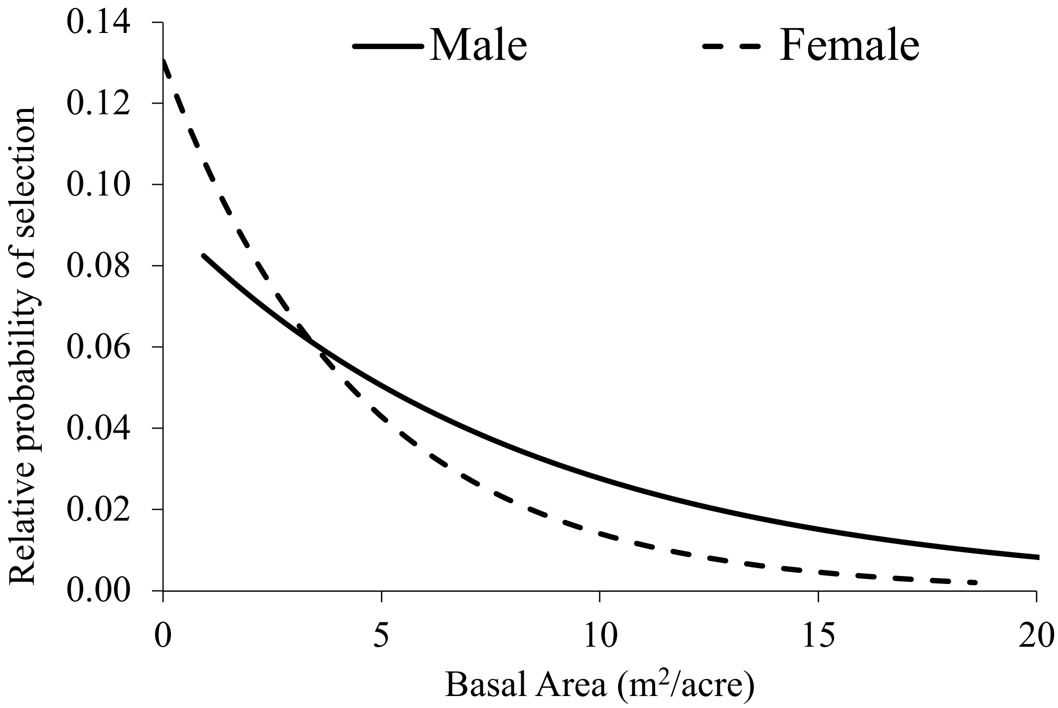
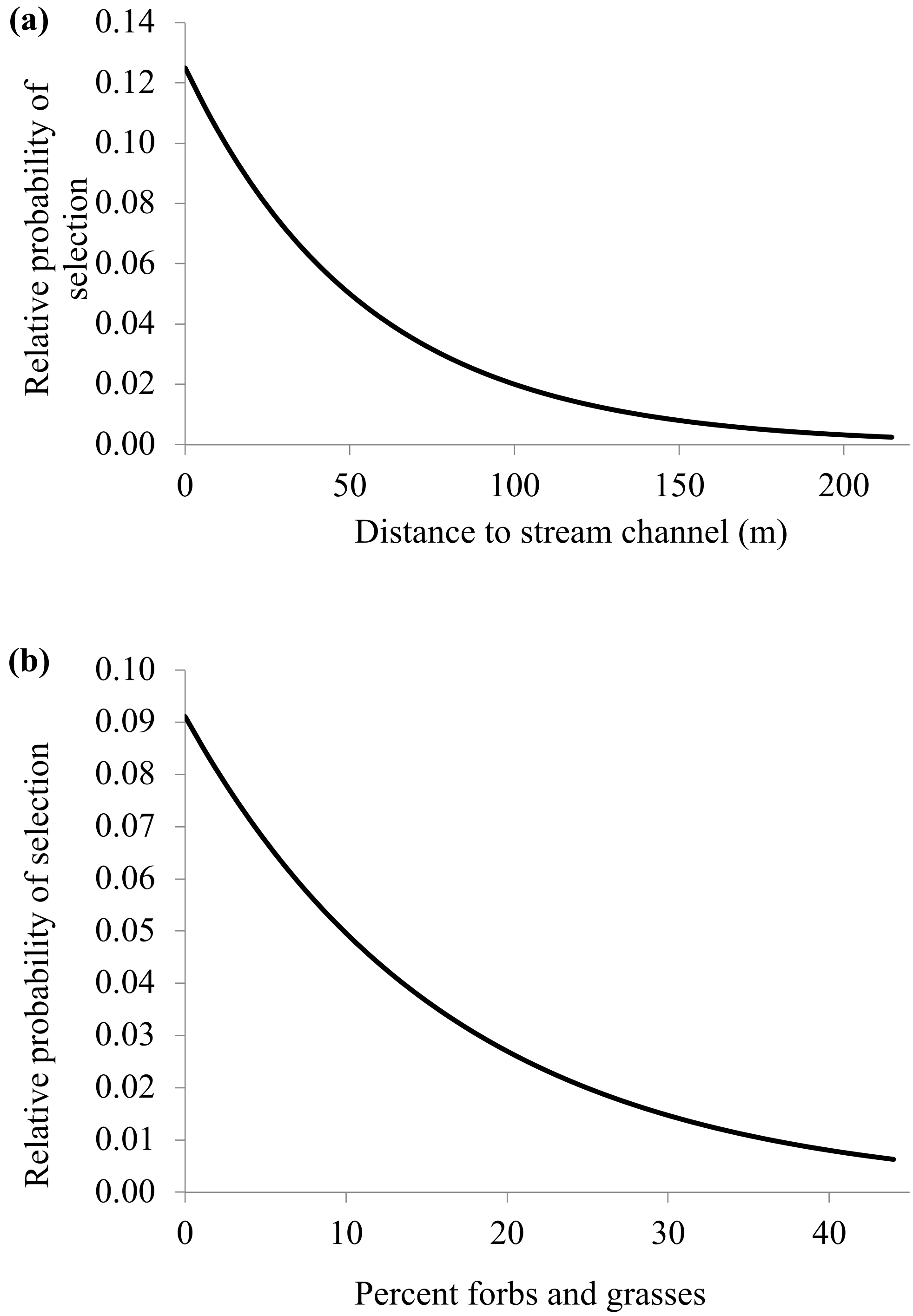
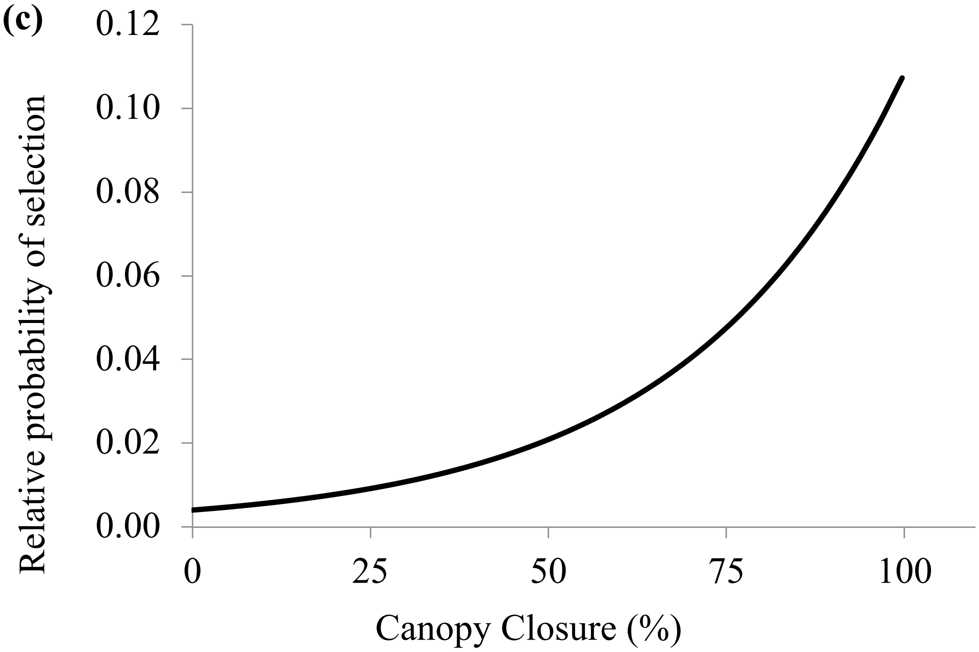


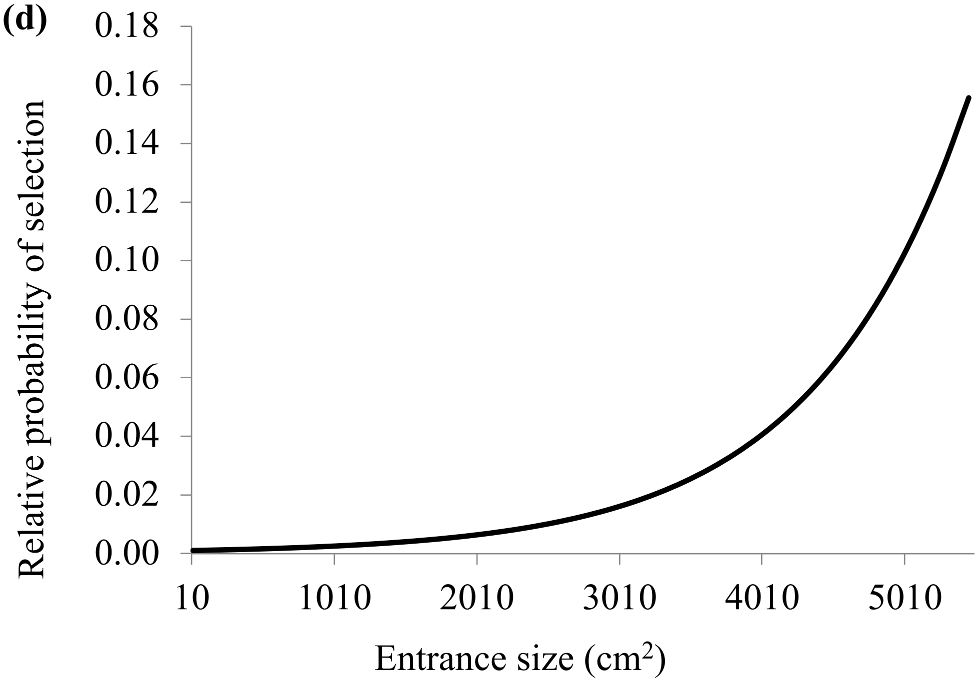
Fig. 4. Relative probability of den site selection in relation to basal area for male (solid line) and female (dashed line) spotted skunks.


(a)
0.14
0.12
0.10
0.08
0.06
0.04
0.02
0.00
Relative probability of selection
0
50
100
150
200
Distance to stream channel (m)
(b)
0.10
0.09
0.08
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0.00
Relative probability of selection
0
10
20
30
40
Percent forbs and grasses

(c)


0.12
0.10
0.08
0.06
0.04
0.02
0.00
Relative probability of selection
0
25
50
75
100
Canopy Closure (%)

(d)


0.18
0.16
0.14
0.12
0.10
0.08
0.06
0.04
0.02
0.00
Relative probability of selection
10
1010
2010
3010
4010
5010
Entrance size (cm^2)

(e)

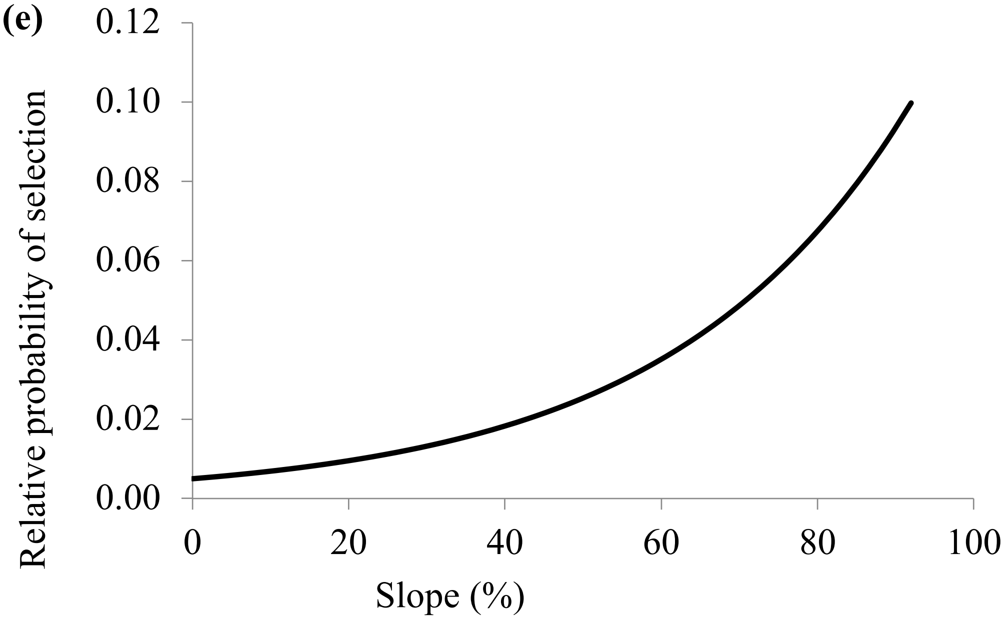


Fig. 5. Male spotted skunk predictive plots indicating the change in probability of den site selection in relation to distance to nearest stream or channel (a), percent forbs and grasses (b), percent canopy closure (c), entrance size (d), and slope (e).